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U. S. NAVAL AIR STATION
PENSACOLA, FLORIDA

RESEARCH REPORT



Joint Report No. NM 001 066.01.04

ROSTRAL PROJECTION PATHWAY
OF THE VESTIBULAR SYSTEM

Emory University School of Medicine
and
U. S. Naval School of Aviation Medicine

U. S. NAVAL SCHOOL OF AVIATION MEDICINE
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JOINT PROJECT REPORT

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ROSTRAL PROJECTION PATHWAY OF THE VESTIBULAR SYSTEM

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SUMMARY

1. Electrical stimulation of the vestibular nerve has excited neural activity which may be tracked to the cerebral cortex in the cat.

2. Recordings from the vestibular nuclei, the midbrain, thalamus and cortex have revealed that the cortical projection is achieved through second order neurons which decussate in the region of the trapezoid and take up a position between the lateral and medial lemnisci to end in the thalamus near the boundaries of the medial geniculate body and the posterolateral ventral nucleus. Third order neurons then project to the posterior bank of the anterior suprasylvian gyrus.

3. In general, the route of projection appears to consist of a group of fibers, which tends to be small and diffuse, and, therefore difficult to identify in degeneration experiments.

INTRODUCTION

A cortical projection area for the vestibular system was postulated for many years before there was experimental evidence for its existence. Among the earlier efforts to localize such an area were those of Spiegel (1) whose experimental approach was that of local application of subconvulsive amounts of strychnine to the cerebral cortex of cats. A locus of strychnine which, when followed by rotation of the animal, produced convulsions was presumed to be the vestibular projection area. The results of that study suggested that the area lay in the vicinity of the posterior ectosylvian gyrus. Studies by Aronson (2), Spiegel (3) and Gerebtzoff (4,5) purported to show that angular acceleration increased the amount of electrical activity in the same area.

A more direct experimental approach was made by Walzl and Mountcastle (6) in 1949 when they used electrical stimulation of the vestibular branch of cranial nerve VIII. This form of stimulation evoked action potentials along a narrow strip of cortex on the anterior bank of the anterior suprasylvian fissure in the cat. It was, therefore, contiguous with the somatic areas anteriorly and the auditory areas posteriorly. Their responses were principally contralateral and had a latency of about 7 msec. No responses were obtained in the area described by Spiegel. Kempinsky (7) in a similar study, corroborated the location of the area but reported bilateral responses with latencies which were considerably longer. In his experiments, preliminary cochlear removal was presumed to result in degeneration of the auditory fibers of the nerve. No adequate controls were available to eliminate the possibility that the cortical response might have been due to propagation through the nervus intermedius or

through intact auditory fibers. The demonstration by Mickle and Ades (8) of auditory responses in the same general cortical area and that of Tunturi (9) on a third auditory area leaves open to question the possibility that non-vestibular fibers may have been responsible for his results.

In a comparative study of the projections of the somatic, auditory and vestibular systems by Mickle and Ades (8), the location of the vestibular area was found to agree well both with Walzl and Mountcastle and with Kempinsky. Latencies were found to be of the order of 7 msec. and the responses were contralateral.

Although many of the connections made by the vestibular system are known, there have been few descriptions of rostrally directed fibers which might be suspected of supplying a projection area on the cerebral cortex. A small bundle of fibers which had origin in the vestibular nuclei was found by von Monakow in 1890, and mentioned by Winkler as Monakow's area (10). This group of fibers was seen to cross the midline just rostral to the nucleus of the VI nerve and to proceed rostrally. A somewhat similar group was followed by Held (11) into the thalamus.

Farrero, Pacella and Barrera (12) have also described degeneration of a small contralateral fiber group which was seen after destruction of portions of the vestibular nucleus complex. The possibility that their results might have been due to the unintentional damage to auditory fibers was not excluded. The ultimate destination of this group of fibers is unknown but it has been presumed that they terminate in or near the medial geniculate body.

EXPERIMENTAL

Young adult cats were prepared surgically under pentobarbital narcosis. The vestibular nerve was approached by fine dissection in the petrous portion of the temporal bone after aspiration of all or a lateral part of the cerebellum. This exposure allowed visualization of the eighth cranial nerve from the end organ to the brain stem. The anatomical separation of the nerve into cochlear and vestibular components near the end organ allowed 1 - 2 mm. of the vestibular nerve to be isolated for stimulation. The facial nerve was destroyed as far medially and proximally as possible.

The vestibular nerve was stimulated through fine silver wires with 100 microsecond rectangular electrical pulses.

Cortical roving electrodes were monopolar chlorided silver wires, operating in conjunction with a stainless steel clip attached to the exposed muscles of the neck. Deep electrodes

were insulated steel needles with exposed tips of about 75 micra diameter. These were placed with a stereotaxic instrument, and the positions checked post mortem with frozen or celloidin sections.

Matched capacitance coupled differential amplifiers with 2 second time constants were used in conjunction with a dual beam cathode ray oscillograph. Patterns were recorded photographically.

RESULTS

Medulla -- Action potentials could be recorded only from the ipsilateral vestibular nucleus complex. Because of occasional mention of fibers which appear to connect the nuclei of the two sides or of possible bilateral innervation (12,13), careful examination of the contralateral group was carried out, but in no case was any activity recorded. Nuclear responses consisted of irregular waves of up to 150 microvolts amplitude, with a latency of 1.0 to 1.25 msec. Their duration was about 4 msec. (Fig. 1A).

Decussation of the second order neurons was found to occur almost immediately. Sagittal section of the brain stem did not obliterate cortical or thalamic responses until the section had been carried down to the level of the nucleus of cranial nerve VI. Needle electrodes thrust into the floor of the fourth ventricle showed contralateral responses at the level of the rostral end of the superior vestibular nucleus. A study of histological sections showing needle tracks in such animals suggested that the crossing was with the trapezoid fibers.

Midbrain -- Exploration in the vicinity of the inferior colliculi revealed that a group of fibers ventral and lateral to the inferior colliculus was activated by vestibular stimulation. Study of histological sections showing needle tracks revealed that the fibers, although somewhat diffusely scattered, lay generally in the area between the medial and lateral lemnisci (Fig. 2B). At the level of the colliculus the action potentials had a latency of 2.5 - 3.0 msec. and frequently showed multiple peaks with a total duration of 4 - 6 msec. (Fig. 1B). No evoked potentials were ever recorded from the surface or within the body of the inferior or superior colliculi.

Diencephalon -- A systematic search of the thalamus revealed that evoked activity could be recorded from a small area lying anteromedial to the medial geniculate body, where it is adjacent to the posterolateral ventral nucleus of the thalamus (Fig. 2C). The total area activated by vestibular nerve stimulation was

about 2 x 2 x 3 mm. in size with its long parameter axial to the brain. The potentials encountered were relatively simple, positive, monophasic waves whose latencies were 4 - 5 msec. with durations of 8 - 10 msec. Amplitudes of 100 to 200 microvolts were usual (Fig. 1D). A careful search of thionin stained sections failed to identify the activated cells with either the medial geniculate body or the posterolateral ventral nucleus, since the strongest responses appeared to originate at the adjacent borders of the two.

Cerebral Cortex -- Cortical action potentials evoked by vestibular nerve stimulation were always encountered on the contralateral side, along a narrow strip of cortex comprising the posterior bank of the anterior suprasylvian gyrus, and occasionally on the extreme anterior bank of the anterior ectosylvian gyrus (Fig. 3). No evoked activity was seen in the middle or posterior ectosylvian areas unless the cochlear branch of the nerve was inadvertently stimulated. The latency of the vestibular responses was 6 - 8 msec. The potentials were nearly always positive with respect to the indifferent electrode, but varied in amplitude and duration with various electrode placements. The greatest potentials were about 500 microvolts and had a duration of 15 - 35 msec. (Fig. 1C).

Minute search of the ipsilateral cortex failed to reveal any evoked activity. Most such checks were made simultaneously with recordings from the contralateral side, using independent amplification channels (Figs. 3 and 4).

Reciprocal stimulation and recording of the cortical and thalamic areas corroborated the projection pathways between the two structures. Stimulation of the thalamic area with minimal currents activated only the vestibular area of the cortex and produced single positive waves with 1.0 - 1.2 msec. latencies. Conversely, weak electrical shocks to the cortical vestibular area resulted in responses in the thalamus. These had approximately the same latency but were rarely above 100 microvolts in amplitude.

DISCUSSION

The cortical projection pathway of the vestibular system appears to follow closely that of the auditory, but without the complex bilateral relationships of that system. The decussation of the fibers at trapezoid level, the course of the tracts near the lateral lemniscus, the close association in the thalamus and cortex combine to suggest reasons for the failure of their identification by histological methods. In addition, the apparent poverty of fibers in the vestibular projection and evidence of their diffusion among adjacent structures renders the system particularly difficult to study by the usual means.

Special identification of the vestibular from auditory projections is seen at several levels. There is no connection of the vestibular system with the inferior colliculi; there is a separate and definable cortical area of projection and there are no bilateral connections in this system.

The thalamic relay point in this system does not seem to be histologically distinct. The location of the activated area bears anatomical contiguity to that of hearing, but, in addition, to that of the pinna and of more caudal somatic reception. Without identifying characteristics of the vestibular cells, conjecture would place them in more direct relationship to those of the medial geniculate body.

Certain possibilities of error are inherent in experiments involving electrical stimulation of the vestibular nerve. Its close association with the cochlear nerve renders differential stimulation unusually difficult. The presence of aberrant or normally occurring auditory fibers on the vestibular branch similar to the ramus cochleo-saccularis described by Hardy (14) has evidently accounted for many failures in otherwise good preparations. Controls on either the electrical spread of the stimulus or stimulation of aberrant auditory fibers have consisted in demonstration of failure of responses to occur in either the inferior colliculus or primary auditory area.

Inadvertent stimulation of the facial nerve introduces a second source of error. Although Kempinsky (7) investigated the problem of afferent fibers in the facial nerve and failed to find interference with recordings at the cortical level, this possibility must be considered. Confusing cortical responses have been seen in the present experiments through the production of facial movements which were reflected to the brain stem and cortex. In this case, response latencies were unusually long, often amounting to 10 to 20 msec. Removal of much of the proximal portion of the facial nerve eliminated these responses.

Leakage of stimulus current to the Trigeminal nerve seems unlikely in those preparations where the adjacent auditory branch was not stimulated.

It is obvious that stimulation of the entire vestibular nerve does not provide information which will specify the nucleus within the vestibular complex which is the origin of neurons for rostral projection. Attempts at differential stimulation of the nuclei themselves have been uniformly unsuccessful. Microscopic study of the area in which decussation occurs suggests that many of the fibers take origin in the superior nucleus.

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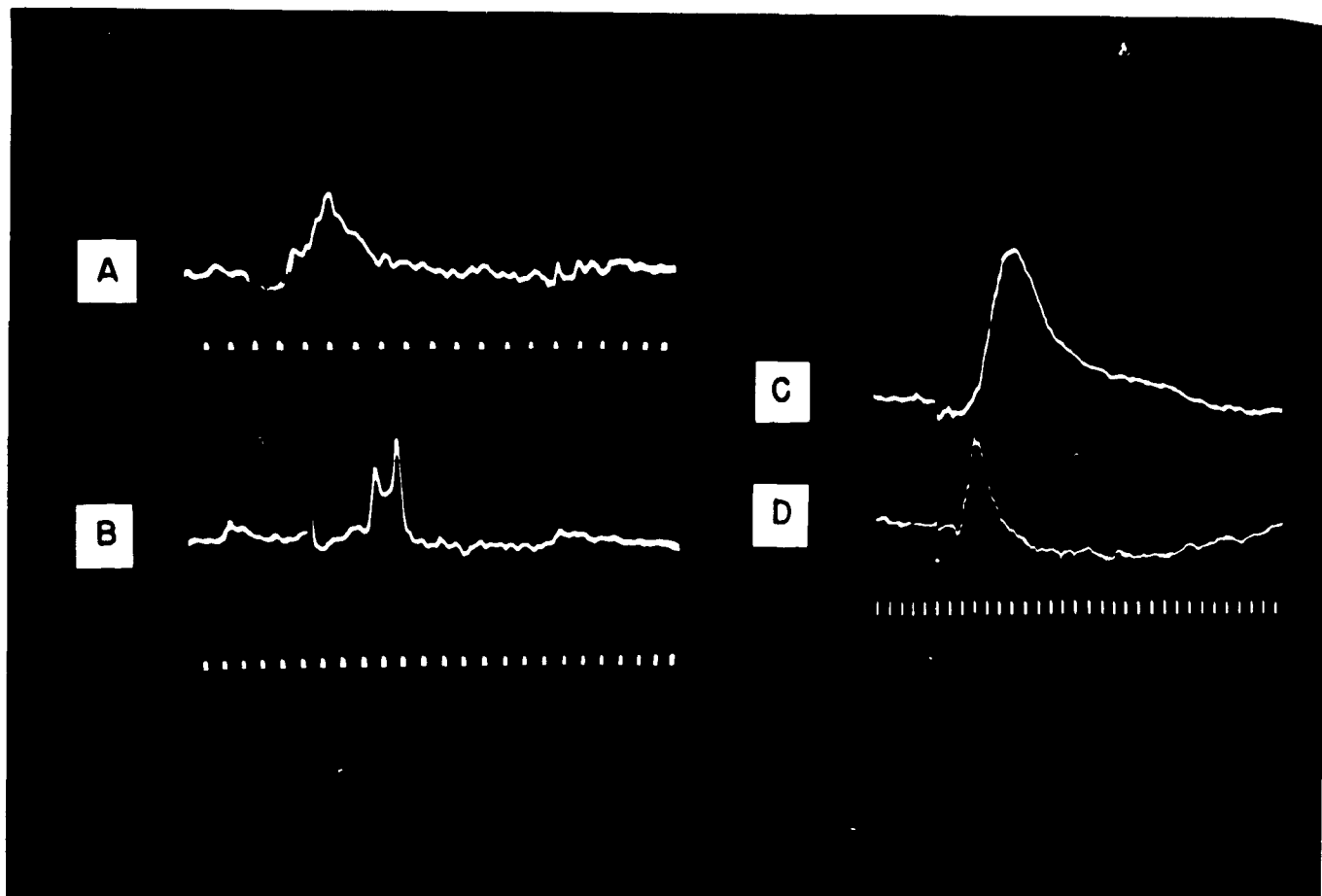


Fig. 1. Oscillographic recordings from vestibular pathway. A: ipsilateral vestibular nucleus complex. B: lateral and ventral to the contralateral inferior colliculus. C: cerebral cortex. D: thalamus. Time, A and B - 1 msec; C and D - 2 msec. C and D taken simultaneously with dual beam oscillograph.

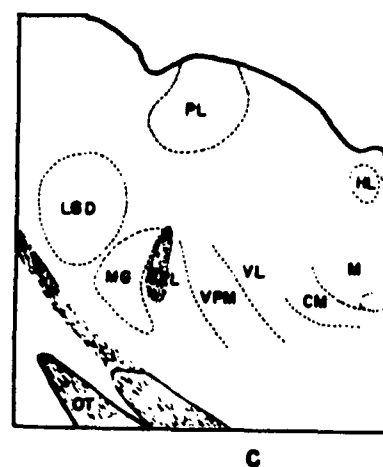
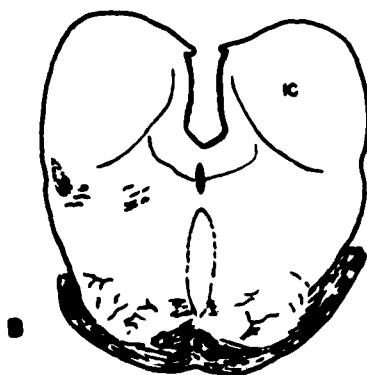
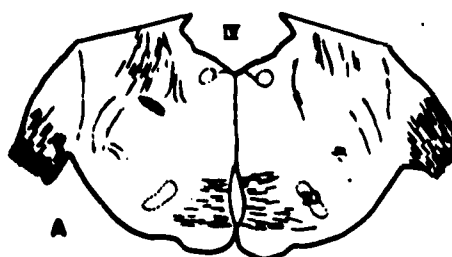


Fig. 2. Positions of vestibular pathway. Areas of strongest response are shown in shaded regions. Stimulation contralateral to pathway. A: 2 - 3 mm. rostral to Superior vestibular nucleus. B: at the level of inferior colliculus. C: thalamus.



Fig. 3. Cortical field of response to contralateral vestibular nerve stimulation. Positive is up.



Fig. 4. Recordings from cortex with ipsilateral vestibular nerve stimulation. These recordings were made at the same time as those shown in Fig. 3, using duplicate channel of recording.